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Research Article

The behaviour of recently-hatched caddis larvae from temporary water bodies in the British Isles*

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Abstract

Caddisflies use four basic methods to ensure that newly-hatched larvae become aquatic insects.

1. One is to lay the eggs underwater so larvae can start a free life immediately after hatching.
2. Another method is to lay the eggs above water and the hatched larvae fall or wriggle into the water.
3. Caddisflies from waters that dry out in summer often have a female diapause gradually becoming sexually mature and often do not lay their clutches until late summer or autumn, when rising water levels flood the eggs. The hatched larvae develop into pupae by March-May, from which adult caddisflies hatch again emergence beginning in spring.
4. Some caddisflies from waters that dry out lay in summer and those eggs hatch soon after laying so it is as a larva that they survive the dry period.

Key Words

behaviour, Britain, eggs, larvae, early instars, Trichoptera

Introduction

Wiggins (1973) is the classic paper on the caddis of temporary pools. One significant life cycle adaptation is to have adults that emerge in spring before the waterbodies dry up and they survive to lay in late summer or autumn. The females have undeveloped ovaries whose maturing is under day-length control. Novak and Sehnal (1963, 1965) and Denis (1981) are well-known papers that studied this. The other adaptation is to lay egg masses from which larvae do not emerge until thoroughly wetted by the waterbody refilling, which occurs in autumn in the British Isles, but where the pools are filled with melting snow, as in Canada, that wetting does not take place until spring.

Hiley (1978) mentioned that larvae of temporary waterbody caddis might hatch before the water returned, due to a transient flooding event. He found that he could hatch larvae from these egg masses and, if kept damp, the newly-hatched larvae survived immobile for many weeks and resumed activity once fully wetted. By contrast, newly-hatched larvae from eggs of species that normally lay underwater did not rest if just kept damp and expired in a few days.

Observations

During caddis surveys in July, the Wallace family (Ian, Brenda, Graham and Matt) have come across limnephilid egg masses which look like those of the usual type for temporary waterbodies in sites which held no free water. *Limnephilus luridus* Curtis and *Rhadicoleptus alpestris*

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(Kolenati) were the species concerned. Captive females of the phryganeid *Hagenella clathrata* (Kolenati) also from peat bogs, lay at that time too, as does *Limnephilus pati* O'Connor from fens. Finding egg-masses in July in sites such as these challenges the classic model. The females involved must have had only a short diapause or probably none at all for *Rhadicoleptus* (Hiley, 1978) and *Hagenella*.

More significantly different is that the larvae escaped from the egg jelly of collected and captive-laid masses before the time water would have returned to their site. However, it is not known if these summer-laid egg masses could survive with their larvae in situ, until autumn, as collecting them and examining them could have disturbed their equilibrium and induced larvae to move and initiate hatching which involves liquefying the jelly.

In *Glyphotaelius pellucidus* (Retzius), the liquefaction of the egg jelly and subsequent escape of the larvae from it have been mentioned several times, for example, Otto (1986) and Crichton (1987). After escaping from the jelly, the hatched larvae must frequently land on soil rather than into water, if the re-wetting of the water body has been delayed. They are presumed to burrow into the bottom, but details are not available. Berté and Pritchard (1982, 2011) studied the liquefaction of the jelly in the North American *Nemotaulius hostilis* (Hagen). The mechanism is not fully understood. After being laid, the outer layer dehydrates to form a "cortex" which, for a while, maintains the integrity of the egg mass when the rest of the jelly has become more fluid after the larvae have hatched within it. Egg masses of other temporary waterbody caddis have been found by the Wallace family with the larvae concentrated at the bottom of the egg mass, but where the "cortex" has not yet ruptured. Berté and Pritchard (1998, 2011) noted that egg masses of species that lay underwater do not develop a cortex and the internal structure of the jelly matrix also differs (Bichierai and Gaino 1987).

Micropterna lateralis (Stephens) has been observed adopting a different strategy for passing summer. Larvae were found in ditches that dried-up over summer. In captivity, these pupated and adults emerged in May before a time when the water had completely dried up in their habitat. However, the adults did not diapause after emergence, but mated and laid rather soft jelly egg masses around stones in their rearing tank. The eggs developed and the larvae hatched and they could be reared to a larger stage. However, in the field, their waterbodies dried up.

An "experiment" was subsequently devised as follows.

In early June, two hatching egg masses, some of whose larvae had made cases, together with the water from their rearing washing-up bowl, were poured into a plant pot of garden soil which was placed in the shade and sporadically watered over the summer. In early September, the soil was submerged in a large bowl of water which was kept aerated. From an estimated 200 larvae poured into the pot of garden soil, around 20 emerged from the soil after re-wetting and subsequently developed; this may seem a small proportion, but the larvae had little time to position themselves in the soil.

Discussion

Hiley (1978) thought that being able to rest as instar 1 would be very useful for temporary waterbody caddis that had hatched due to, for example, a downpour temporarily flooding their site. A few species may use instar 1 as a preferred over-summering stage.

Bogs and fens would seem to have a very amenable damp substratum for survival of small larvae. The sites may actually have the disadvantage of being too wet for temporary water-body egg masses, as that would probably cause the larvae to escape even if it was just into a water film (Hiley 1978).

Early laying and early hatching do not seem to apply to all individuals. Hiley (1978) noted eggs of *L. luridus* being laid in early September. Crichton (1971) grouped this species with many others with a diapause and autumn laying. For *Micropterna lateralis* in Sweden, Svensson (1972) found the ovaries were at a late stage of maturation when they emerged in spring, but in the south of France, Bouvet (1976) reported that they entered an ovarian diapause after emergence and Higler (2008) for the Netherlands also attributes a diapause. This variability may also be reflected in Britain as Hiley (1978) reports only some had developed ovaries when they emerged.

Many limnephilids of permanent waters lay eggs near the water's edge or on riparian vegetation and rely on hatching larvae falling in or waves or a slight water level rise to cover them and wash larvae into the water. They too must, on occasions, hatch before being continuously submerged, due to egg mass disintegration or a flooding event and would need to have a suitable strategy to survive in soil. The egg-laying site preferences of aquatic British Limnephilidae and Phryganeidae are shown in Table 1.

The in-substratum behaviour of recently-hatched caddis larvae has not been studied. For example, do they make a case, do they burrow into the substratum and do they have a different physiology to larger larvae? Response of cased caddis larvae to drying has not been studied often. Wichard (1989) gives a first overview of caddisflies from waters that dry up in summer in Central Europe (12 Limnephilidae and 1 Phryganeidae). Wichard believes that the ability to respond to low oxygen levels by producing more gill filaments could be significant in these challenging waterbodies. Survival is reported for *M. lateralis* by Erzinger et al. (2019) and for *Limnephilus coenosus* Curtis and *L. vittatus* (Fabricius) by Zamora-Munoz and Svensson (1996) and, for *M. sequax*, by Stubbington et al. (2016). *Oligostomis reticulata* (Linnaeus) was reported by Sommerhauser et al. (1997) to over-summer as very small larvae in sealed-up cases in the dry stream bottom; this was quiescence not diapause as they rapidly re-activated if wetted and the few larvae trapped in remnant pools remained active, survived and developed.

Table 1. Preferred egg-laying sites of aquatic British Limnephilidae and Phryganeidae.

Group 1 laying underwater or into water
All Phryganeidae, except *Hagenella clathrata* and *Trichostegia minor*; *Apatania muliebris*; *A.auricula*? and *A. wallengreni*?; *Drusus annulatus*; *Ecclisopteryx dalecarlica*; *Anabolia nervosa*; *Halesus radiatus*; *H. digitatus*?; *Hydatophylax infumatus*?; *Melampophylax mucoreus*? *Mesophylax impunctatus*?; *Micropterna lateralis*, *M. sequax*?; *Potamophylax* species.
Group 2 laying above or by the side of permanent water
Chaetopteryx villosa; *Glyphotaelius pellucidus*; *Halesus radiatus*; *Limnephilus affinis*; *L. binotatus*?; *L.borealis*?; *L. centralis* mountain pools; *L. decipiens*; *L. exricatus*; *L. fuscicornis*?; *L. hirsutus*?; *L. ignavus*?; *L. lunatus*; *L. marmoratus*; *L. nigriceps*; *L. pati*? *L. politus*; *L. rhombicus*; *L. stigma* mountain pools; *L. subcentralis*; *Micropterna* species ?; *Nemotaulius punctatolineatus*.
Group 3 laying well away from free water
Hagenella clathrata summer hatcher; *Trichostegia minor*; *Ironoquia dubia*; *Anabolia brevipennis*; *Glyphotaelius pellucidus*; *Grammotaulius nigropunctatus*; *G. nitidus*?; *Limnephilus affinis*; *L. auricula*; *L. bipunctatus*; *L. centralis*; *L. elegans* summer hatcher?; *L. flavicornis*; *L. griseus*; *L. hirsutus*; *L. incisus*; *L. lunatus*; *L. luridus* summer hatcher on occasions; *L. marmoratus* summer hatcher on occasions; *L. pati* summer hatcher; *L. sparsus*; *L. stigma*; *L. tauricus*; *L. vittatus*; *Rhadicoleptus alpestris* summer hatcher; *Mesophylax aspersus*; *Stenophylax* species.

Note that these species may have a different behaviour in other countries and even within this country so may appear in more than one section. References for individual species can be found in Wallace and O'Connor (2023). A '?' indicates that there are no direct observations for that species.

The Annulipalpian species, *Plectrocnemia conspersa* (Curtis), utilises temporary streams and marshes. Their eggs do not seem well adapted to drying, but a strategy could be hatching from autumn- or spring-laid eggs before the waterbody dries and passing summer in the substratum as a small larva.

Conclusion

The behaviour and physiology of recently-hatched caddis larvae has been little studied. Species may adopt several strategies to ensure the survival of their larvae.

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